•综述•

基于类胡萝卜素着色的鸟类羽色多样性形成机制

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摘要: 人们对动物体色的研究由来已久。作为一类让生物呈现出多变色彩的重要色素, 类胡萝卜素可以在鸟类的羽毛、鸟喙和皮肤等体表组织中沉积, 产生红、橙、黄、粉、紫等颜色。类胡萝卜素不能在鸟类体内合成, 需从食物中摄取, 进而在体内完成吸收、运输、代谢和沉积等一系列过程, 才能用于羽毛着色。与类胡萝卜素着色相关的生理及遗传调控机制一直备受关注, *BCO2*、*SCARB1*和*CYP2J19*等影响类胡萝卜素在鸟类羽毛中着色的关键基因, 推动了对羽色遗传调控机制的深入认识。本文介绍了鸟类可利用类胡萝卜素的主要类型和基本特征, 综述了类胡萝卜素着色相关的生理过程以及调控基因研究的最新进展, 旨在增加对鸟类羽毛中类胡萝卜素着色过程和相关遗传机制的理解。

关键词: 类胡萝卜素; 羽色; *CYP2J19*; *BCO2*; *SCARB1*; 代谢

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The formation and mechanism of plumage color diversity based on carotenoid pigmentation

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ABSTRACT

Background & Aims: Animal coloration has long been a topic of interest. As one of the most colorful groups in the world, birds exhibit a wide diversity of plumage pigmentation patterns. Carotenoid, an important component contributing to vivid colors in many avian species, can be deposited in avian integument and produce red, orange, yellow, pink and purple coloration, which can serve as an honest signal of individual condition in mediating social and mating interaction. Therefore, carotenoid pigmentation is an ideal phenotypic trait for understanding the diversity of plumage coloration under a variety of evolutionary pressures and constraints. Most significantly, this complex coloration mechanism provides a variety of opportunities for the evolution of plumage coloration driven by natural and sexual selection. In this review, we highlight the current advances in the mechanisms underlying carotenoid-based coloration in four physiological processes involved in carotenoid coloration in birds. We also introduce the interaction of carotenoid pigment and microstructural coloration, and the ecological forces that drive the evolution of carotenoid coloration.

Progresses: We summarized the biochemical pathways of dietary carotenoids absorption, transportation, metabolism and deposition in birds, all of which may affect feather coloration as condition-dependent traits. We further reported a biochemical modification pathway of the yellow dietary carotenoids and conversion to red ketocarotenoids *in vivo*, which gives birds more opportunities to become colorful. Still, the physiological and genetic mechanisms related to carotenoid processing remain uncertain. With the development of high-throughput sequencing technology, recent breakthroughs have revealed some genes that control carotenoid pigmentation, which has shed light on the molecular basis of carotenoid-based coloration. These genes, such as *CYP2J19*, *BCO2*, *SCARB1*, play an important role in the carotenoid coloration in feathers, and lay the foundation for our understanding of the genetic mechanism of carotenoids

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in the process of feather coloration.

Prospects: This review provides a helpful foundation for understanding the biochemical mechanisms underlying bird coloration. In addition, we have put forward questions in the field that require urgent attention: (1) How do different physiological pathways interact to form and maintain the color diversity in birds? (2) What factors regulate the metabolism and deposition of carotenoids during the growth of bird feathers, which makes the occurrence of carotenoid plumage present a specific temporal and spatial pattern? (3) How does the plumage dichromatism caused by the difference in carotenoid coloration occur and maintain?

Key words: carotenoid; plumage color; *CYP2J19*; *BCO2*; *SCARB1*; metabolism

鸟类是世界上色彩最丰富的生物类群之一，它们多变的羽色可通过色素沉积、结构色以及两者的组合形成(Hill & McGraw, 2006)。这种复杂的着色机制为羽色在自然选择和性选择驱动的演化过程提供了多样的机会(Shawkey & D’Alba, 2017)。类胡萝卜素作为鸟类中重要且广泛存在的一类色素，能够显示出红、橙、黄、粉、紫等颜色，并且可以通过与结构色或其他色素的相互作用，产生更为广泛的色彩(Hill & McGraw, 2006; LaFountain et al, 2015)。与内源合成的黑色素不同，类胡萝卜素不能在鸟类体内从头合成，而需要从饮食中摄取，进而通过吸收、运输、代谢以及在体表组织中沉积等过程，使鸟类的皮肤、羽毛与喙着色(Weaver et al, 2018)。此外，一些鸟类可在体内对摄取的类胡萝卜素进行生化加工，改变类胡萝卜素的光学特性，从而使羽毛呈现出更加丰富的羽色(Koch et al, 2016)。

类胡萝卜素是许多细胞完成基本生命活动必需的多效性分子。除了用于鸟类羽毛的着色，类胡萝卜素还可作为抗氧化剂、免疫调节剂和光保护剂参与视觉、免疫等多种重要的生理过程中(Ligon et al, 2016)。一般认为，与类胡萝卜素相关的性状受到环境因素(例如食物)的影响，具有条件依赖性(condition-dependence)，产生和维持这种性状通常需要较高的生理代价(Kodric-Brown & Brown, 1984; von Schantz et al, 1999)。当资源有限时，类胡萝卜素在体内的分配与利用会受限于个体自身的健康程度与生理发育阶段。因此，与类胡萝卜素相关的性状通常被作为“诚实”信号来反映个体质量，这是性选择理论的重要假说之一(Zahavi, 1977; Hamilton & Zuk, 1982)。

早期关于鸟类羽色遗传调控机制的研究主要集中于黑色素，其生化合成通路相对明确，*MC1R*、*TYR*、*ASIP*等黑色素基因会对鸟类羽色的变异产生重要影响(Tobita-Teramoto et al, 2000; Kerje et al,

2003; Nadeau et al, 2008)。相比而言，由于对脊椎动物类胡萝卜素着色的生理过程和调控通路缺乏系统和深入的认识，对于类胡萝卜素着色遗传机制的研究长期止步不前。

近十几年来，得益于高通量测序技术的发展，通过比较基因组学与演化发育学研究，一些与类胡萝卜素代谢和修饰相关的基因在鸟类中被发现。这些对鸟类羽毛中类胡萝卜素的着色具有重要作用的基因，为我们理解类胡萝卜素在羽毛着色过程中的遗传调控机制奠定了基础(Lopes et al, 2016; Cuthill et al, 2017; Gazda et al, 2020a)。

本文总结了鸟类中类胡萝卜素着色的最新研究进展，从类胡萝卜素的生化特性、着色过程、遗传调控机制等角度，综述了鸟类中类胡萝卜素的着色机制与演化过程，并展望了未来的研究发展方向。

1 类胡萝卜素的生化特征与基本类型

1.1 类胡萝卜素的生化特征

作为一类广泛存在的天然色素，类胡萝卜素几乎完全由细菌、藻类、真菌以及高等植物合成(Olson & Owens, 1998)。动物组织中存在的类胡萝卜素属于C40四萜烯分子，以交替的C=C双键为特征，跨越由8个异戊二烯单元组成的碳骨架(LaFountain et al, 2015; Toews et al, 2017)，这种碳氢骨架既能以非环化的形式存在，也可以在单侧末端或双侧末端进行环化(惠伯棣, 2005; 高广琦等, 2016)。饮食中大多数类胡萝卜素的末端都具有含1个双键的六碳环(紫罗酮环, ionone ring)，当这个双键在C5-C6位置，则此端环为β-紫罗酮环；当双键在C4-C5位置，则该端环为ε-紫罗酮环(图1A) (Hill & Johnson, 2012)。

类胡萝卜素为脂溶性，不溶于水，其化学结构直接影响它们呈现出的颜色。类胡萝卜素的光吸收特性主要取决于具有共轭双键的中心链，这种化学结构使类胡萝卜素倾向于吸收短波长(蓝色和紫色)

图1 类胡萝卜素的化学结构与分类。(A)类胡萝卜素的两种端环: β -紫罗酮环与 ϵ -紫罗酮环; (B)动物中6种具代表性的类胡萝卜素。修改自von Lintig等(2020)。

Fig. 1 Chemical structures and categories of carotenoids. (A) The chemical characteristics of two different end-groups: β -ionone ring and ϵ -ionone ring; (B) Six representative carotenoids in animals. Figure adapted from von Lintig et al (2020).

的可见光, 反射出较长波段的光, 使类胡萝卜素呈现出红色、橙色或黄色(Britton, 1995; Olson & Owens, 1998)。一般认为, 共轭链的长度、双键的数量以及与其他分子的互作均会影响到类胡萝卜素的颜色(Britton, 1995; Toews et al, 2017)。类胡萝卜素吸收光的波长随共轭链增长、双键数量增加而变短, 发生反射率红移, 故呈现出的颜色更趋近于红色(Prum et al, 2014)。除此之外, 当类胡萝卜素与相关蛋白结合时, 会产生紫色、绿色和蓝色等色彩(Shawkey & D'Alba, 2017)。鸟类体表组织中的类胡萝卜素可通过有机溶剂分离出来, 并可使用分光光度法、光谱法、色谱法等进行分析(Olson & Owens, 1998)。

1.2 类胡萝卜素的主要类型

自然界中存在超过1,000种类胡萝卜素, 在动物组织中已经鉴定出数百种(Britton, 1995; Toews et

al, 2017)。鸟类日常摄取的类胡萝卜素虽仅有十几种, 但一些鸟类可以通过对类胡萝卜素进行内源性修饰来增加类胡萝卜素的多样性(LaFountain et al, 2015)。到目前为止, 鸟类体内已鉴定出30余种类胡萝卜素分子, 并且仍有新的色素在不同类群中被陆续发现(Hill & McGraw, 2006; LaFountain et al, 2010, 2013; Prum et al, 2012)。

已知可用于鸟类着色的类胡萝卜素依据化学结构可分为两类: 胡萝卜素类(carotene)和叶黄素类(xanthophyll)(图1B)。第一类是纯碳氢化合物, 主要包括 α -胡萝卜素(α -carotene)、 β -胡萝卜素(β -carotene)和番茄红素(lycopene)等; 第二类是氧合类胡萝卜素, 主要包括叶黄素(lutein)、玉米黄质(zeaxanthin)和 β -隐黄质(β -cryptoxanthin)等(Svensson & Wong, 2011)。

由于部分类胡萝卜素是脊椎动物合成维生素A

的主要来源(von Lintig, 2010), 也常据此分为维生素A原类胡萝卜素(pro-vitamin A carotenoid)和非维生素A原类胡萝卜素(non pro-vitamin A carotenoid)(Weaver et al, 2018)。前者主要包括 α -胡萝卜素、 β -胡萝卜素和 β -隐黄质等, 其碳链末端至少具有一个未被修饰的 β -紫罗酮环, 因此可裂解合成维生素A; 后者主要包括叶黄素和玉米黄质, 其碳链两端的环均被氧化, 不具有合成维生素A的活性, 因此不能作为维生素A的前体(von Lintig et al, 2020)。

2 鸟类利用类胡萝卜素着色的过程

在鸟类中, 胡萝卜素的着色主要涉及4个生理过程, 包括类胡萝卜素在消化系统中被摄取、在循环系统中运输、在上皮组织或肝脏中进行代谢, 以及在体表着色组织中沉积(图2), 其中任一过程出现遗传变异均有可能影响到色素最终的沉积, 一些重要基因的序列突变或表达水平的改变即会对表型产生巨大的影响(Hill et al, 1994; Hubbard et al, 2010; Orteu & Jiggins, 2020)。Walsh等(2012)总结了脊椎动物中与类胡萝卜素着色过程相关的11个候选基因; Gao等(2018)确定了48个与脂质相关基因(lipid-related gene)具有直接或间接联系的候选基因, 这些基因可能与鸟羽中广泛的类胡萝卜素沉积有

关。对于一些拥有类胡萝卜素加工和修饰能力的鸟类, 由于长期以来人们对修饰膳食类胡萝卜素的酶知之甚少, 导致研究这些功能的遗传机制成为一项艰巨的任务。直到近期, 关于类胡萝卜素如何被代谢为新形式方面才取得了一些新的进展。

类胡萝卜素代谢通路在不同动物类群间具有生理和遗传上的保守性, 由于涉及该过程的基因可能具有多效性, 即部分受体蛋白可能同时会承担其他基础的生理功能, 因此一些鸟类中类胡萝卜素相关的表型多态性也有可能是由基因的调节突变(regulatory mutation)引起的, 不涉及到基因功能的完全丧失(Van der Horst et al, 2009; Walsh et al, 2012)。

2.1 类胡萝卜素的吸收与运输

类胡萝卜素的吸收发生在胃肠道中, 是指类胡萝卜素向淋巴或血液运动的过程, 其中类胡萝卜素从食物基质中释放以及在脂质相中溶解是吸收过程中的关键步骤(Erdman et al, 1993; Yeum & Russell, 2002)。类胡萝卜素是高度疏水的化合物, 它们不能直接溶解于缺乏两亲性分子的水性介质, 因此, 饮食中的脂质可以很好地帮助类胡萝卜素分散到胃肠道中, 继而以乳状液(emulsion)的形式散布在消化液中(Kotake-Nara & Nagao, 2011)。在胆汁

图2 类胡萝卜素在羽毛中着色的主要过程。修改自Yeum和Russell (2002), Hill和Johnson (2012)。

Fig. 2 Main process of carotenoid-based coloration in bird feathers. Figure adapted from Yeum & Russell (2002) and Hill & Johnson (2012).

和脂肪分解酶的作用下, 类胡萝卜素被溶解在由游离脂肪酸、胆汁盐、磷脂和单酰基甘油构成的混合胶束(mixed micelle)中(Nagao, 2011)。随后, 胶束形式的类胡萝卜素在肠上皮跨膜转运蛋白作用下, 吸收进入肠上皮细胞(Scita et al, 1993)。脊椎动物与类胡萝卜素结合的转运蛋白主要包括清道夫受体蛋白家族的SCARB1 (SR-B1)与CD36以及ABC转运蛋白家族的ABCG5/G8复合体等(Yu et al, 2004; During et al, 2005; Kotake-Nara & Nagao, 2011)。清道夫受体蛋白家族是具有胞外结构域的糖基化跨膜蛋白, 包含大型的疏水通道, 其中SCARB1的转运功能在果蝇、金丝雀(*Serinus canaria*)等物种中均得到了证实(Kiefer et al, 2002; Toomey et al, 2017)。ABCG5/G8复合体仅在肠上皮细胞和肝细胞中表达, 在限制膳食固醇吸收的过程中起到重要作用, 并且该功能在哺乳动物中已得到验证(Yu et al, 2004); ABCG5在人类中的多态性与叶黄素的生物利用度有关, 并且ABCG5可能参与到叶黄素和玉米黄质反向运输至肠腔的过程中, 该过程通过耗能的主动运输来完成(Herron et al, 2006)。

在鸟类的肠上皮黏膜细胞中, 类胡萝卜素被脂蛋白包装成乳糜微粒(chylomicron)分泌到淋巴, 继而进入血液循环系统(During et al, 2005; Kotake-Nara & Nagao, 2011)。在血液中, 乳糜微粒被脂蛋白脂肪酶降解, 类胡萝卜素残余到达肝脏进行贮存、代谢及包装再分泌(Yeum & Russell, 2002)。肝脏再分泌的类胡萝卜素需要与脂蛋白(lipoprotein)结合进入血液循环中(Parker, 1996), 其中胡萝卜素类在血浆中的运输需要与低密度脂蛋白(low density lipoprotein, LDL)结合, 其他极性较强的类胡萝卜素(例如叶黄素类)则倾向与高密度脂蛋白(high density lipoprotein, HDL)结合(Erdman et al, 1993)。鸟类肝脏中的转运蛋白ABCA1负责向肝外输出类胡萝卜素和其他脂类, 该过程对于类胡萝卜素与HDL结合是重要的限速步骤, 可能影响到类胡萝卜素着色。通过对具有白色皮肤的家鸡“WHAM”突变体的研究, 发现其ABCA1基因出现错义突变, 虽然饮食中的叶黄素和玉米黄质仍可被肠道和肝正常吸收, 但从肝脏向外周组织转运的过程显著缺失, HDL水平显著降低, 最终导致白色皮肤表型产生(Attie et al, 2002; Connor et al, 2007)。

脂蛋白被靶组织摄取是一个有选择的过程, 通

常需要被靶组织(皮肤、毛囊、视网膜等)上的受体(例如SCARB1与CD36)识别, 继而以被动运输的方式被靶组织摄取, 促进类胡萝卜素向细胞内的转运(Sakudoh et al, 2013)。SCARB1可作为高密度脂蛋白受体来介导靶组织类胡萝卜素着色, 其编码基因SCARB1发生突变可能会破坏类胡萝卜素的转运过程。Toomey等(2017)发现金丝雀的白色隐性突变个体与红色或黄色的品种相比, 其组织中类胡萝卜素的含量非常低。结合遗传图谱法, 发现白色隐性等位基因是由于SCARB1的剪切供体存在点突变, 导致数量最多的剪切异构体出现异常剪切, 丧失了转运类胡萝卜素的功能, 最终导致类胡萝卜素无法在体表组织中积累着色。

2.2 类胡萝卜素的代谢与沉积

体表组织选择性摄取的类胡萝卜素以脂滴的形式积累, 在羽毛中与角蛋白结合, 呈现出黄或红等颜色(Brush, 1990)。这些体表衍生物既可以直接从食物中获取、沉积未经修饰的黄色膳食类胡萝卜素(dietary carotenoid), 或者沉积内源修饰后的类胡萝卜素, 获得更丰富的颜色(Stradi et al, 1996)。例如, 绝大部分雀形目的红色羽毛都是黄色膳食类胡萝卜素内源转化为红色酮基类胡萝卜素(ketocarotenoid)的结果(Davies, 1985)。McGraw等(2006)提出雀形目中类胡萝卜素的着色机制存在3个层次:

(1)沉积黄色膳食色素(dietary yellow pigments): 将未经修饰的黄色类胡萝卜素(例如叶黄素和玉米黄质)沉积到皮肤、羽毛和鸟喙中(Hill & McGraw, 2006)。这是色素沉积中最简单的机制, 部分蜡嘴雀和森莺等类群会通过这种方式使羽毛呈现黄色(Hill & Johnson, 2012)。

(2)沉积黄色转化色素(yellow converted pigments): 将黄色类胡萝卜素在体内转化为其他黄色色素的途径, 包括将膳食叶黄素和玉米黄质, 经过脱氢生成3-脱氢叶黄素(3-dehydrolutein)以及金丝雀黄素(canary xanthophyll) A和B (Hill & McGraw, 2006)。3-脱氢叶黄素在肝脏中生成, 金丝雀黄素生成位置尚不清楚, 推测在靶组织(例如毛囊)中合成(Hill & Johnson, 2012)。美洲金翅雀(*Carduelis tristis*)会采用此种方式来生成并在羽毛中沉积金丝雀黄素A和B (McGraw et al, 2005; Weaver et al, 2018)。

(3)沉积红色转化色素(red converted pigments):

酮化酶(ketolase)将黄色类胡萝卜素氧化成红色的酮基类胡萝卜素。这个过程涉及的代谢机制比较复杂,并已在多种红色的雀形目鸟类中被发现(Hill & McGraw, 2006)。3-羟基海胆酮(3-hydroxy-echinenone)是金翅雀亚科最主要的酮基类胡萝卜素,它是 β -隐黄质中一个 β -紫罗酮环被氧化后的产物。雄性美洲家朱雀(*Haemorhous mexicanus*)的红色羽毛主要以3-羟基海胆酮进行着色,其个体间黄色到红色的变化与酮基类胡萝卜素的含量成正相关(Inouye et al, 2001; McGraw et al, 2006)。在鸟类羽毛中发现的其他酮基类胡萝卜素还包括海胆酮(echinenone)和角黄素(canthaxanthin),它们分别是 β -胡萝卜素一个或两个端环被氧化的产物,人工培育的红色型金丝雀利用角黄素进行着色(Lopes et al, 2016)。在其他鸣禽中,由玉米黄质两个端环氧化形成的虾青素,也是常见的一种红色酮基类胡萝卜素。雄性猩红比蓝雀(*Piranga olivacea*)的红色繁殖羽为虾青素着色(Hudon, 1991);雄性主红雀(*Cardinalis cardinalis*)的红色羽毛则由虾青素、角黄素、 α -皮黄素(α -doradexanthin)与金盏花红素(adonirubin)等共同沉积着色(McGraw et al, 2003)。

酮化酶修饰类胡萝卜素的过程一般被认为发生在肝脏与视网膜中,也有研究认为该过程也会在毛囊等沉积部位发生(del Val et al, 2009; Ge et al, 2015; Mundy et al, 2016)。Hill等(2019)通过对美洲家朱雀的肝线粒体进行生理学测量,以及对酮化酶进行分子建模,证实类胡萝卜素的酮化发生于线粒体内膜,且红色类胡萝卜素羽色与线粒体的功能和活性密切相关。

尽管类胡萝卜素的内源性修饰早在数十年前已被提出,但相应的功能基因仍不清楚。近年来两项研究独立地发现了同一种编码细胞色素P450酶的基因——*CYP2J19*,可以将黄色的膳食类胡萝卜素转化为红色的酮基类胡萝卜素,是影响鸟类着色的重要酮化酶基因(Lopes et al, 2016; Mundy et al, 2016)。Mundy等(2016)以具有黄色喙部的斑胸草雀(*Taeniopygia guttata*)突变体为研究对象,利用不同表型个体的基因组SNP数据,通过连锁图谱(linkage mapping)将决定颜色差异的关键突变定位于8号染色体的*CYP2J19*基因座。*CYP2J19*在突变体的喙部几乎不能表达,导致突变体具有黄色的喙,而不是野生型红色的喙,证实*CYP2J19*是类胡萝卜素酮化

酶的重要候选基因;Lopes等(2016)使用金丝雀与黑头红金翅雀(*Spinus cucullata*)的杂交后代——红色型金丝雀(red-factor canary)鉴定出相同的候选基因,并发现*CYP2J19*的表达量在红色型金丝雀的皮肤和肝脏中显著上调,进一步证实*CYP2J19*是介导鸟类红色类胡萝卜素着色的关键酮化酶基因。此外,酮化酶催化产生的酮基类胡萝卜素不仅会使羽毛呈现红色,同时也贡献于鸟类红色视网膜油滴,因此该基因在视觉系统中功能保守(Twyman et al, 2018a)。

尽管编码酮化酶的基因已被揭示,但是有关*CYP2J19*参与的着色机制在不同物种中的普遍性未完全得到验证。首先,该基因在不同物种间的拷贝数存在差异,例如在红色型金丝雀中,*CYP2J19*为单拷贝基因,而在斑胸草雀中为双拷贝。其次,在不同物种中的高表达部位也存在差异。红色型金丝雀中的肝脏和皮肤都可以检测到*CYP2J19*的高表达;而在斑胸草雀中,*CYP2J19*主要在红色的喙部表达;Twyman等(2018b)通过对16种红色与黄色非洲织布鸟的比较研究,发现*CYP2J19*在红色织布鸟肝部的表达量要显著高于其他色型的织布鸟,但在皮肤中几乎检测不到该基因的表达,表明鸟类还可以通过增加*CYP2J19*在肝脏中的表达量来提升体内酮基类胡萝卜素的含量,进而形成红色的羽毛。此外,通过对红背细尾鹩莺(*Malurus melanocephalus*)的研究发现睾酮可以上调*CYP2J19*的表达水平,增强酮基类胡萝卜素的代谢与着色能力,从而提升了个体所获得的性选择优势与繁殖成功率,为理解内分泌信号对*CYP2J19*基因表达及羽色的调控机制提出了新的证据(Khalil et al, 2020)。

鸟类体内的类胡萝卜素处于参与沉积着色与分解的动态过程中, β -胡萝卜素加氧酶(β -carotene oxygenases)作为参与类胡萝卜素分解的一类酶,在不同动物中被广泛研究,对类胡萝卜素的代谢具有重要影响。到目前为止,在哺乳动物和鸟类中已经鉴定出两个 β -胡萝卜素加氧酶基因:*BCO1*和*BCO2*,其中*BCO1*酶可通过裂解维生素A原类胡萝卜素,生成维生素A用于视觉系统与免疫系统;与*BCO1*酶相比,*BCO2*酶除了可以裂解维生素A原类胡萝卜素,还可以裂解更多种的类胡萝卜素,是调节类胡萝卜素沉积的重要候选基因(Vaage & Boman, 2010)。

*BCO1*和*BCO2*发生突变对多种生物中的类胡

胡萝卜素代谢具有重要影响, 这些突变可能会导致动物组织中类胡萝卜素的积累增加, 从而产生色素积累的表型, 直接影响动物的着色(Toews et al, 2017)。Eriksson等(2008)证明家鸡腿部的黄色皮肤是由*BCO2*顺式调控元件的突变所引起。该突变抑制了*BCO2*在家鸡皮肤中的表达, *BCO2*酶无法把黄色类胡萝卜素分解为无色产物, 导致类胡萝卜素在家鸡腿部皮肤中的积累。该研究认为家鸡的黄腿性状是由同为黄腿的姊妹种——灰原鸡(*Gallus sonneratii*)基因渗入而获得的, 打破了长期以来关于红原鸡是家鸡唯一祖先的固有认知。不同于上述*BCO2*的突变形式, 在对具有红色喙部的金丝雀突变体进行的研究中, *BCO2*的单个非同义突变会消除*BCO2*酶的裂解活性, 导致红色类胡萝卜素在喙部积累(Gazda et al, 2020b)。除此之外, 近缘种间或两性别间的羽色差异也可能与*BCO2*有关。通过对两种在类胡萝卜素着色区域呈现出羽色差异的森莺进行比较基因组分析, 发现*BCO2*位于少数的高分化区域中, 表明该基因很可能与类胡萝卜素着色差异有关(Toews et al, 2016); 在人工培育的马赛克型金丝雀(mosaic canary)雌雄个体中, *BCO2*在体表组织中活性不同, 导致类胡萝卜素在性别间差异性降解, 从而产生性二态现象(Gazda et al, 2020a)。

值得注意的是, 尽管与*BCO2*相关的性状看似容易获得和丢失, 增添了表型的多样性和不稳定性, 然而, *BCO2*酶功能缺失或减弱的个体可能需面临类胡萝卜素在器官中过度聚积的风险。例如在对美洲金翅雀的研究中发现, 高浓度类胡萝卜素会导致其体内的肌酸激酶增加, 加速骨骼肌衰竭, 对其飞行能力造成影响(Huggins et al, 2010)。因此, 在考虑*BCO2*突变带来的鲜艳羽色在性选择中的优势时, 同时也需要考虑过度积累类胡萝卜素需承担的生理代价。

3 类胡萝卜素色素与羽毛微结构的互作

类胡萝卜素除了可以单独使鸟类着色外, 在某些情况下, 还可以和羽毛的微结构发生相互作用, 增加鸟类羽毛着色的方式。Shawkey和D'Alba (2017)提到类胡萝卜素与结构互作的3种情况, 会对鸟类呈现出的颜色起到潜在影响, 它们分别为: (1)无序的角蛋白微结构会对类胡萝卜素着色产生影响; (2)有序的微结构会对类胡萝卜素着色产生影响; (3)类

胡萝卜素与其他蛋白质的相互作用。

鸟类的羽毛是由 β -角蛋白构成的纤维性蛋白多聚物, 类胡萝卜素沉积于角蛋白形成的角质层中, 产生颜色(郑光美, 2012)。由于羽毛的蛋白结构和色素均会与入射光线发生相互作用, 角蛋白中较厚的随机气孔阵列会散射更多光线, 从而增加羽毛的亮度, 因此有些羽毛即使呈现出典型的色素色, 仍可能兼具结构色成分(Shawkey & D'Alba, 2017)。例如, 美洲金翅雀亮黄的羽色是类胡萝卜素与通过角蛋白增强反射的光线共同作用产生的(Shawkey & Hill, 2005), 这是无序角蛋白结构影响鸟类类胡萝卜素着色的典型案例。

有序的纳米结构包括规则排布的海绵状角蛋白或黑素体等。鸟类羽毛非虹彩的绿色主要由该着色模式产生, 例如绿阔嘴鸟(*Calyptomena viridis*)呈现出的绿色由黄色类胡萝卜素与准有序的角蛋白阵列共同作用产生(Prum et al, 2014); 此外, 部分鸟类中暗绿的羽色由分布在羽毛不同位置的类胡萝卜素与黑素体结合的方式产生。黑素体指表皮色素细胞中分泌形成的黑色素颗粒, 其形态种类多样, 可为实心或空心、球状或棒状、扁平或圆形等, 并可以形成单层薄膜或多边形阵列等结构, 使得入射光在黑素体与其他材质的界面发生散射(Maia et al, 2012)。黑素体的着色模式在鸚鵡中最为典型。鸚鵡摄取膳食类胡萝卜素, 但并不把它们沉积在羽毛中, 而是沉积一类谱系特有的黄色多烯醛色素——鸚鵡黄素(psittacofulvins) (Cooke et al, 2017; Mundy, 2018)。在不同颜色的虎皮鸚鵡(*Melopsittacus undulatus*)中, 除黄色和灰色个体外, 其他所有色型的羽毛在角质层上覆盖了一层黑素体, 因此鸚鵡黄素与这种结构发生互作后增加了色彩饱和度, 并可以产生更为广泛的色彩(D'Alba et al, 2012)。由于鸚鵡黄素和类胡萝卜素都属于脂色素, 因此以上羽色形成机制对研究类胡萝卜素与黑色素相互作用对羽色的影响具有重要启发。

羽毛中的类胡萝卜素通常会结合蛋白质来保证其化学性质的稳定, 当类胡萝卜素与结构蛋白形成复合物时, 原本的黄色、橙色或红色可以变为蓝色、紫色或绿色(Weesie et al, 1995)。例如在呈现出鲜亮红色的美洲红鸚(*Eudocimus ruber*)、橙红色的玫红丽唐纳雀(*Piranga rubra*)与具有紫色羽毛的白眉紫须伞鸟(*Iodopleura isabellae*)中, 红色、橙红与

紫色羽毛中的类胡萝卜素均主要为角黄素,而不同的蛋白质-角黄素结合模式导致了羽毛反射光谱的变化(Mendes-Pinto et al, 2012)。

4 类胡萝卜素羽色的演化历史及驱动力

由于类胡萝卜素的易降解性,在鸟类羽毛化石中尚未发现类胡萝卜素着色的证据。对于类胡萝卜素羽色演化历史的认识主要来源于系统发育研究。基于全球所有鸟类羽色重建类胡萝卜素着色的演化历史,发现类胡萝卜素着色在鸟类中经历了多次起源,最早一次起源发生于约5,600万年前(古新世)雀形目的共同祖先。然而,在雁形目、鸱形目等十余个已经证实存在类胡萝卜素羽色的类群中,类胡萝卜素着色的能力是在中新世以后独立演化而来的(Thomas et al, 2014; Twyman et al, 2016),这暗示现生鸟类在羽毛中沉积类胡萝卜素的能力可能是趋同演化的结果。在现存鸟类中,雀形目利用类胡萝卜素着色的物种比例最高,演化历史最长,是当前研究关注的重点类群。基于鸟类羽色来源的成分鉴定与祖先状态重建分析,发现雀科的祖先最有可能先利用未经修饰的膳食类胡萝卜素对羽毛进行着色,此后藉由类胡萝卜素关键代谢基因的突变,部分物种获得了在体内对类胡萝卜素进行修饰的能力,它们就不会再将膳食类胡萝卜素直接用于羽毛着色(Ligon et al, 2016),这种渐进式的过程表明,类胡萝卜素羽色的形成与调控机制经历了由简单到复杂的多个演化阶段。

类胡萝卜素着色一直以来都被认为是性选择研究的经典模式(Morehouse, 2014; Weaver et al, 2018)。比较系统发育分析表明,霸鹟小目雄性羽色的快速进化是驱动类胡萝卜素羽色多样化的主要动力,表明种间性选择信号的差异与类胡萝卜素羽色的演化模式具有显著相关性(Cooney et al, 2019)。昂贵信号理论(costly signaling principle)提出的资源权衡假说(resource trade-off hypothesis, RTOH)是对类胡萝卜素羽色作为诚实性选择信号的重要解释(Weaver et al, 2017)。基于该假说,用于着色的类胡萝卜素会占用原本用于对抗细胞活性氧(ROS)的抗氧化资源,因此只有高质量雄性才能负担资源分配的代价——在产生鲜艳色彩信号的同时,仍然可以满足正常生存的需求(Morehouse, 2014)。然而,对于

类胡萝卜素羽色能否作为诚实信号尚未得到一致认可。有观点认为其他分子也可承担抗氧化剂的功能,减少类胡萝卜素的消耗,弱化了类胡萝卜素羽色作为“诚实信号”的作用(Hartley & Kennedy, 2004);甚至关于类胡萝卜素资源是否“昂贵”的问题至今也还存在争议(Hill & Johnson, 2012; Koch et al, 2018)。Hill (2011)提出了新的共享通路假说(shared-pathway hypothesis),如果类胡萝卜素代谢与细胞呼吸效率之间存在密切的生理联系,则可以直接解释许多类胡萝卜素性状的演化,而不完全受限于资源权衡假说(Johnson & Hill, 2013)。由于红色酮基类胡萝卜素合成的过程与线粒体密切相关,因此与其相关的性状尤其适合检验共享通路假说,近来对斑胸草雀和红交嘴雀(*Loxia curvirostra*)的研究也支持了共享通路假说的预期(Cantarero et al, 2020a, b)。

5 展望

类胡萝卜素着色的相关表型是鸟类社交的重要信号,也是理解鸟类羽饰在多种演化压力与制约因素下多样化的理想表型。近年来依赖于高通量测序技术,在鸟类中新发现的类胡萝卜素基因型-表型对应关系,使得类胡萝卜素着色的遗传机制黑箱被逐步打开,将为基于类胡萝卜素着色表型的性选择与自然选择研究提供更充分的科学证据。尽管如此,我们对控制类胡萝卜素信号遗传机制的理解仍不完善,例如:(1)个体内不同的生理途径如何相互作用,以形成并维持这些信号;(2)在鸟类羽毛的生长过程中,类胡萝卜素的代谢和沉积过程受到何种因素的调控,使类胡萝卜素羽色的发生呈现出特定的时空规律;(3)由类胡萝卜素着色差异引起的羽色性二态如何发生并维持等。随着功能基因组学与进化发育生物学研究方法的发展,我们相信未来有望发现更多与类胡萝卜素着色相关的功能基因与代谢、调控通路,有助于揭开鸟类利用类胡萝卜素着色的演化历史与遗传机制的全貌,从而加深我们对鸟类羽色多样性起源与维持机制的理解,更好地认识自然选择与性选择对鸟类表型演化的作用。

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